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The hystricomorphy of the Bathyergidae, as determined from ontogenetic evidence

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Abstract

Two younger fetuses of *Bathyergus janetta* and *Georychus capensis* showed small bundels of the anterior zygomatico-mandibular muscle penetrating the infraorbital canal. This infraorbital muscle is missing in adult bathyergids with the exception of *Cryptomys hottentotus*. It is an old and as yet unsettled question whether the bathyergids are primarily 'protrogomorphous' or 'hystricomorphous' rodents. The transitory embryonic relics of infraorbital muscles described in this study seem to favour the latter opinion. Our results support the position that the Bathyergidae should be grouped together with the other hystricognathous and hystricomorphous rodents.

Introduction

The relationship of African 'hystricomorphous' rodents is one of the major open questions of the phylogenetic systematics of rodents (Luckett and Hartenberger 1985). Within this context the status of the Bathyergidae (mole-rats) is of considerable relevance. With the exception of *Cryptomys*, all genera of this family show relatively small infraorbital foramina which are not penetrated by a portion of the anterior zygomatico-mandibular (or anterior medial masseter) muscle; there is an old and as yet unsettled debate whether this 'protrogomorphy' is a primitive or derived character state. Tullberg (1899), Ellerman (1940), Morlok (1983) and Wood (1985) adhere to the position that the Bathyergidae primarily possess a small infraorbital foramen, and that *Cryptomys* is showing a secondary specialization; according to Wood (1985) *Cryptomys* demonstrates the evolutionary development of 'hystricomorphy' in statu nascendi and "may currently be about to do the same thing" as did the Miocene *Bathyergoides* and many other rodents in parallel. The

opposite opinion has been maintained by WINGE (1923), LANDRY (1957), LAVOCAT (1973), and LUCKETT and HARTENBERGER (1985); they assume that hystricomorphy has been secondarily lost within the Bathyergidae, and that only *Cryptomys* retains the primitive condition. It becomes evident from these controversial views, that the classification of the mole-rats in particular, and of the African 'hystricomorphs' in general, depend to some degree on the morphological evaluation of the 'infraorbital complex'.

Considering the supposed taxonomic value of this 'infraorbital complex', it may be surprising that not more detailed information is available about its comparative anatomy. TULLBERG (1899), who extensively studied the chewing muscles of rodents, did notice only nerves and vessels passing through the infraorbital foramen in adult specimens of *Georychus capensis*. But he did mention that *Georychus coecutiens* has a wider infraorbital foramen, "und dass ein kleiner Teil des Masseter medialis dieses Foramen hier in der That durchsetzt" (p. 79); however, this taxon has been subsequently classified as subspecies of *Cryptomys hottentotus* (ALLEN 1939; ELLERMANN et al. 1935). WEBER (1928) obviously did not recognize the specific muscle arrangement in *Cryptomys*, because he stated for the Bathyergidae in general: "Durch den Canalis infraorbitalis passieren nur Nerven und Blutgefäße, keine Portion des Masseter medialis" (p. 288).

The chewing musculature of *Cryptomys hottentotus* was reexamined by BOLLER (1970). He showed that in this species a muscle of considerable size passes through the enlarged infraorbital foramen. Whereas TULLBERG (1899) had called this portion 'Portio anterior masseteris medialis', BOLLER (1970) preferred to follow KRAPP (1965) and others with regard to the nomenclature. The medial portion of the masseter muscle is considered as an independent 'm. zygomaticomandibularis'; parts of the anterior portion of this muscle may penetrate the infraorbital foramen as 'pars infraorbitalis' or as 'm. maxillo-mandibularis'. MORLOK (1983) confirmed the results of BOLLER, although he noticed some minor differences in his specimens of *Cryptomys*. MORLOK dissected adult specimens of all living Bathyergidae, and he was unable to find remains of a 'pars infraorbitalis' in genera other than *Cryptomys*.

It is widely accepted that the morphological analysis of skull structures should include their ontogenetic development (GAUPP 1906; STARCK 1967). The morphogenetic process is a constituent factor of any character complex. Experience shows that embryonic stages are by no means always 'recapitulatory', instead they are adapted to their specific modes of life; however, comparative embryology often is a valuable source of information, which should not be neglected by phylogenetic systematics. The analysis of ontogenetic data should follow the rules and principles lined out by BOCK (1981) for problems of evolutionary morphology.

Comparative embryology has the disadvantage of its data being mostly difficult to obtain. Ontogenetic stages have to be prepared as histological serial sections. In many cases plate reconstructions have to be made from these. Due to lack of suitable material and due to restricted capacities of histological laboratories one is confined to one or few stages of each species; these stages are usually not fully developmentally equivalent to those of other species; nevertheless useful comparisons can be made. Serial sections always provide very detailed insight into the relationship of hard and soft tissue structures and elucidate structural arrangements at a microscopic level.

Material and methods

In connection with a more comprehensive study of craniogenesis in African hystricomorphous rodents (SCHRENK, in prep.) we were able to prepare serial sections of three developmental stages of *Bathyergus janetta* Thomas and Schwann, 1904, which were generously loaned by the Zoology Department of the Witwatersrand University, Johannesburg (Prof. CREWE). The youngest stage had a crown-rump length (CRL) of 13 mm and a head length (HL) of 8 mm; the next stages had CRL of

21 mm and 48 mm, and HL of 12 mm and 20 mm, respectively. Our fetus of *Georychus capensis* Pallas, 1778, had a CRL of 30 mm and a HL of 16 mm; this specimen has been loaned by the Hubrecht Laboratory, Utrecht (Dr. BANGMA). The state of differentiation of this specimen is in between the two older stages of *Bathyergus*. Cleaned skulls of bathyergids have been studied and measured in the following institutions: Senckenberg Museum, Frankfurt/Main; British Museum of Natural History, London; American Museum of Natural History, New York; Smithsonian Institution, Washington D.C. All curators have kindly permitted us to study their collections.

For one of the fetuses of *Bathyergus* (CRL 21 mm) a plate-reconstruction with a magnification of 40 times has been prepared; this model was used for preparing Fig. 1.

Results

Fig. 1 shows the lateral side of the plate reconstruction of *Bathyergus janetta* (CRL 21 mm). In addition to the skeletal structures, the anterior zygomatico-mandibularis muscle (or anterior medial masseter), the infraorbital nerves and vessels, the nasolacrimal duct, and the eyeball have been modelled. The diameters of the slightly enlarged infraorbital foramen are 0.4 by 0.2 mm. A number of infraorbital nerve branches and the infraorbital artery pass through the lower and medial part of the foramen. In its dorsolateral portion, a thin bundle of muscle fibres penetrates the foramen (Fig. 2). It consists of
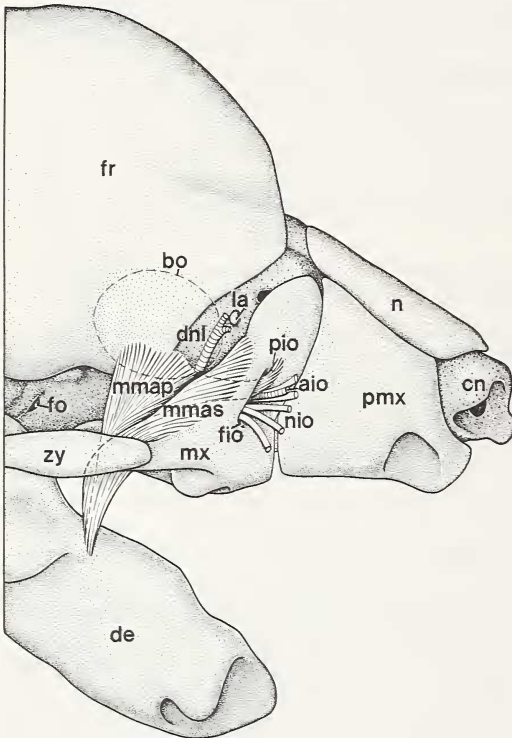

Fig. 1. Lateral aspect of the muzzle of a fetus of *Bathyergus janetta* (CRL 21 mm); the drawing has been made from a plate reconstruction of 40 times magnification. Only the skeletal elements of the facial skull and the soft tissues of the 'infraorbital complex' are shown. A small bundle (pars infraorbitalis) of the deep portion of the medial anterior masseter muscle (or anterior zygomatico-mandibularis muscle) penetrates the infraorbital canal in addition to the infraorbital nerves and vessels. The structures of the cartilaginous endocranium are dark stippled, the overlying exocranial bones are light stippled. Abbreviations: aio – arteria infraorbitalis; bo – bulbus oculi; cn – cupula nasi anterior; de – dentale; dnl – ductus nasolacrimalis; fio – foramen infraorbitale; fo – foramen opticum; fr – frontale; la – lacrimale; mmap – masseter medialis anterior profundus; mmas – masseter medialis anterior superficialis; mx – maxillare; n – nasale; nio – nervus infraorbitalis; pio – pars infraorbitalis of the masseter medialis anterior profundus (zygomatico-mandibularis anterior); pmx – premaxillare; zy – zygomaticum

about a dozen fibres and its maximum vertical diameter is about 0.1 mm. It originates from the lateral surface of the maxillary bone in front of the infraorbital foramen, and posteriorly joins the deeper portion of the anterior zygomatico-mandibular muscle (stippled outlines). We consider this small muscle bundle as a pars infraorbitalis of the anterior zygomatico-mandibularis muscle. Whereas the superficial portion of this muscle originates from the anterior and inferior border of the orbital margin, its deep portion springs mainly

from a ventrally projecting orbital process of the frontal bone; both portions insert with a common tendon at the mandible. The deep portion with its infraorbital bundle bridges the nasolacrimal duct. A tiny lacrimal bone is developed near the lacrimal canaliculi. The infraorbital muscle bundle is present on both sides, but it is somewhat smaller on the right side.

In our youngest specimen of *Bathyergus* (13 mm CRL) no distinct muscle bundle is present within the infraorbital foramen. However, a strand of condensed mesenchyme runs in the position where the muscle was to be expected. Since this is a very young fetus in which the tissues are not yet well differentiated, we prefer to interpret this situation as an immature state of development; we suspect that the myotubes of the zygomatico-mandibularis muscle, which is already present, invade the mesenchymatous 'Anlage' of the pars infraorbitalis at a somewhat later stage. In our oldest fetal stage of *Bathyergus* (48 mm CRL), the infraorbital muscle is missing completely; we believe that it is already reduced at this stage. Dissection of an adult specimen of *Bathyergus suillus* (Collection of Prof. STARCK) did not reveal any infraorbital bundle of the strong anterior zygomatico-mandibular muscle. Although we cannot rule out at present the possibility that our fetus with small infraorbital muscle bundles only represents an individual variant, we rather suspect that this muscle is a transitory and shortlived fetal structure. Even a variant of the observed kind would still be of considerable theoretical interest.

It may be added that the older fetus of *Bathyergus janetta* (48 mm CRL) shows a well developed lacrimal bone already partly fused with the maxillary bone. The existence of a distinct lacrimale has been disputed in the literature for the bathyergids; we are now able to state its presence at younger fetal stages.
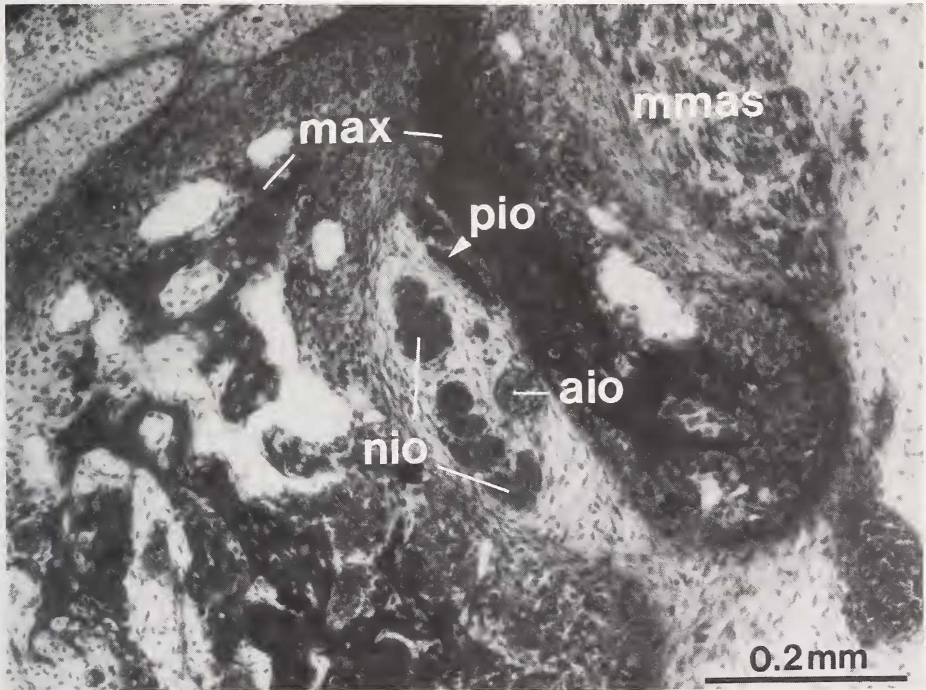

Fig. 2. Histological cross-section through the canalis infraorbitalis of *Bathyergus janetta* (CRL 21 mm); section 17-1-3). The section shows the muscle bundle of the masseter medialis anterior passing through the dorsolateral corner of the infraorbital canal. (Abbrev. the same as in fig. 1)
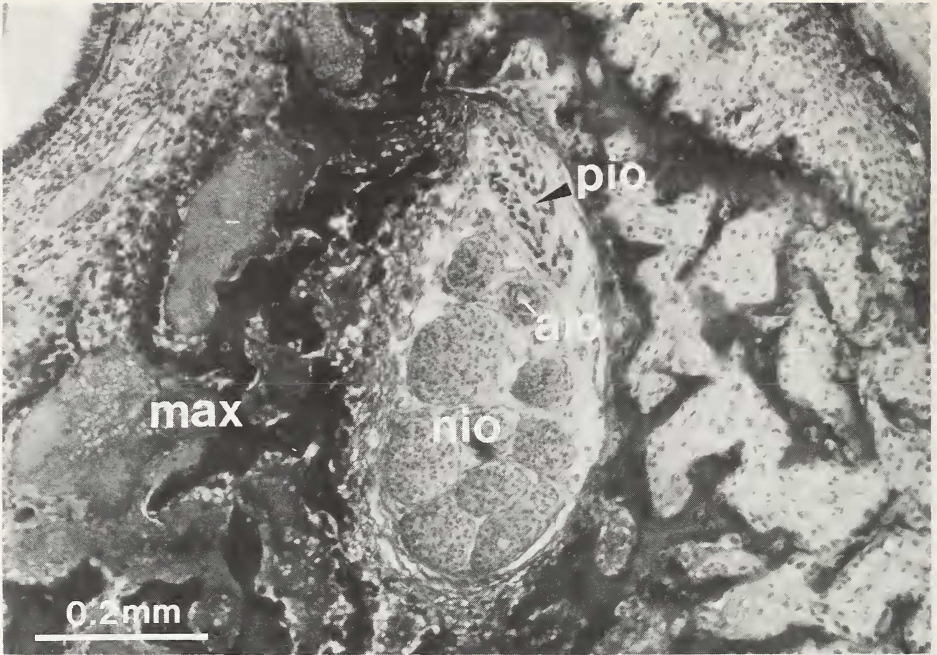
Fig. 3. Histological cross-section through the canalis infraorbitalis of *Georychus capensis* (CRL 30 mm; section 18-4-2). The infraorbital muscle bundle is stronger than in *Bathyergus*, but it is in the same position

The serial sections of a fetus of *Georychus capensis* (30 mm CRL) show that this species temporarily possesses a pars infraorbitalis of the m. zygomatico-mandibularis as well (Fig. 3). On the left side we find a bundle of about 40 fibres with a maximum diameter of little less than 0.2 mm. It originates just at the anterior margin of the infraorbital foramen and passes through the lateral part of its roof and again joins the deep portion of the zygomatico-mandibular muscle. On the right side this muscle bundle is very short and it only invades the posterior end of the infraorbital canal. As MORLOK (1983) has shown, adult specimens of *Georychus* do not possess an infraorbital muscle. From the limited ontogenetic evidence it would seem that this transitory muscle portion is somewhat larger than in *Bathyergus* and that it persists somewhat longer during fetal life.

Since there only exist vague descriptions of the infraorbital foramen in dried skulls of various bathyergids (ELLERMAN 1940), we made an effort to provide more objective data (see table). We have measured a large sample of museum specimens of all genera. Species whose exact taxonomic position is still doubtful are omitted. Greatest height and width have been measured at the anterior opening of the infraorbital canal. The basicranial length (prosthion-basion according to DUERST 1926) was taken as a measure of the skull size. Since skull and body size vary considerably among the bathyergid taxa, an allometric approach was chosen. In the graph (Fig. 4) all parameters have been expressed as natural logarithms.

The graphic presentation of the data shows the smallest species *Heterocephalus glaber* having a relatively small sized infraorbital foramen; intraspecifically its diameters increase rapidly with skull size. *Bathyergus*, *Georychus* and *Heliophobius* are closely grouped together but display a tendency of increasing the foramen in this taxonomic sequence. It seems possible that these small size differences reflect varying degrees of development of the pars infraorbitalis of the zygomatico-mandibular muscle during ontogeny; it is

coincident with this hypothesis that *Georychus* shows a better developed muscle-relic than *Bathyergus*, and that it will be still larger in the not yet known fetuses of *Heliophobius*. It is in accordance with all known data that the infraorbital foramen is especially wide in *Cryptomys*, whose pars infraorbitalis of the m. zygomatico-mandibularis persists throughout life (Boller 1970; Morlok 1983). In the larger species, the slopes of the regression curves are lower than in the small *Heterocephalus*. The standard deviations of all our means are relatively high; this is due to a considerable natural variability of size and form of the foramen, and might also reflect the difficulties in taking standardized measurements.

Discussion

We have shown that fetuses of both *Bathyergus* and *Georychus* possess small bundles of the pars infraorbitalis of the anterior zygomatico-mandibular (or anterior medial masseter) muscle during a short period of their development. It seems to be missing in very young fetuses of *Bathyergus*, and has again disappeared in older fetuses. On the other hand, it is known for a long time that only *Cryptomys* among adult bathyergids shows a large infraorbital canal and persisting infraorbital muscle. In other words, *Cryptomys* is 'hystricomorphous' throughout life, while *Bathyergus* and *Georychus* are 'hystricomorphous' only during a short period of their fetal life. How are these ontogenetic findings to be interpreted?

We do not adhere to the philosophy that embryological data necessarily represent a primitive phylogenetic stage. On the contrary, we have overwhelming evidence from craniogenetic studies that most of the specific skull characters appear at very early stages. Fetal characters have to be submitted to a careful morphological analysis as is necessary for adult characters. In the presented case, however, we believe that the described rudimentary and transitory muscles are most easily explained as 'atavistic repetitions' of an older phylogenetic state; i.e. we believe that bathyergids were primarily hystricomorphous rodents, and that this character complex has been lost secondarily within this group. According to this view, *Cryptomys* is the only genus that has retained hystricomorphy, whereas in other taxa this feature is only shortly expressed in the ontogenetic 'Bauplan'.

But could these small muscles not be 'pioneer fibres' indicating a new and progressive development as has been suggested by Wood (1985)? We can think

Table

This table presents the metric values of the measurements

Means, standard deviations and variances of the skull baselengths, the height and width of the infraorbital foramina of different bathyergid taxa are given

|	n	Skullbase-length prosthion-basion (mm)			Infraorbital foramen height (mm)			width (mm)		
		M	SD	v	M	SD	v	M	SD	v
Heterocephalus glaber	21	18.95	4.381	18.28	0.59	0.125	0.014	0.53	0.101	0.009
Bathyergus janetta & suillus	68	50.62	9.200	83.47	1.73	0.384	0.145	1.51	0.290	0.083
Georychus capensis	32	39.10	4.472	19.38	2.11	0.718	0.499	1.24	0.389	0.147
Heliophobius argenteocinereus	48	33.79	3.155	9.750	1.58	0.268	0.070	1.27	0.229	0.051
Cryptomys hottentotus	94	29.48	5.002	24.76	3.26	0.885	0.776	1.37	0.338	0.113
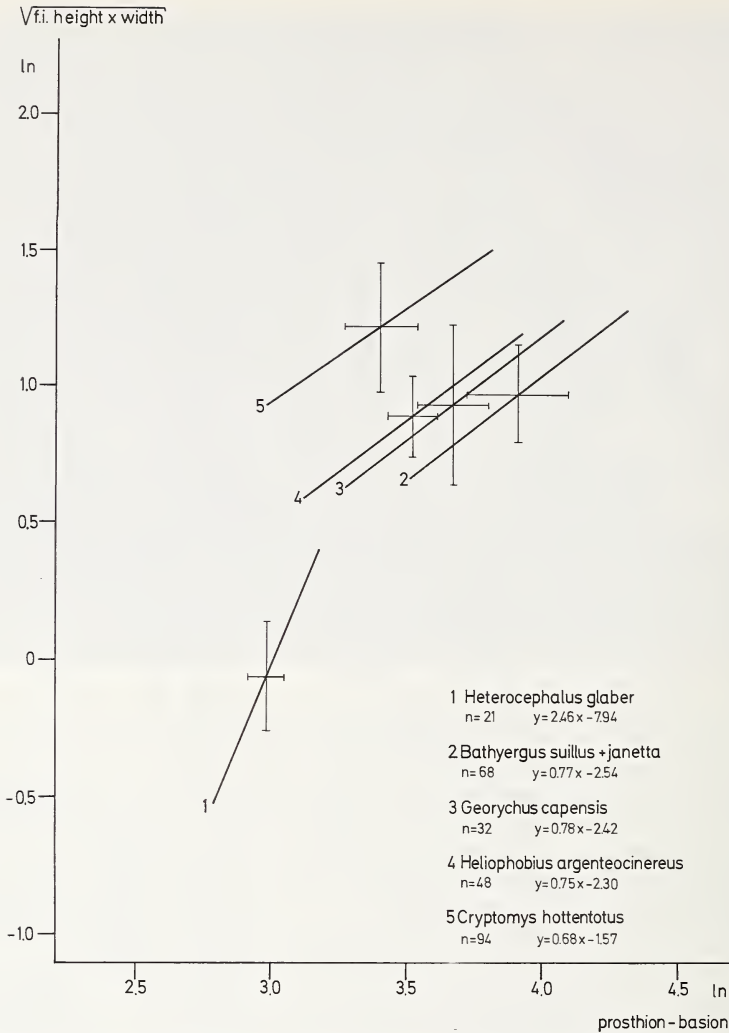
Fig. 4. Graphic presentation of the metric dimensions of the infraorbital foramen in bathyergids. The size of the anterior opening of the foramen is expressed as the square root of the product height and width; the skull size is represented by the prosthion-basion length. All data have been transformed into natural logarithms to compensate for the absolute size differences of the various taxa. The crossed bars indicate the standard deviations of the means; the equations of the regression lines are given in the legend of the figure

of no functional explanation for a small muscle to penetrate the narrow infraorbital canal for only a short ontogenetic period. The small infraorbital muscle in *Bathyergus* (21 mm CRL) has exactly the same origins and connections as are known from adults of *Cryptomys* and other African hystricomorphous rodents; in *Georychus*, its anterior origin is shortened to varying degrees. Bilateral asymmetry of the small muscles supports the view that they are functionally meaningless; indeed a high variability is not atypical for rudimentary structures.

Since we do not properly understand the meaning of an hystricomorphous arrangement of chewing muscles in functional terms, we have even more difficulties to explain the secondary loss of this feature. MORLOK (1983) has reviewed the different opinions on this

problem. *Cryptomys* seems to dig more exclusively with its incisors, whereas the other taxa make more use of their specialized forefeet (NOWAK and PARADISO 1983). We cannot support the arguments of TULLBERG (1899) and of LAVOCAT (1973), according to which the reduction of the bathyergid eyeballs may have resulted in a reduction of the medial masseter and in a strengthening of the temporalis muscle. BOLLER (1970) has recorded very small eyeballs for the hystricomorphous *Cryptomys* (diameter 1–1.5 mm); we have measured in an adult specimen of *Bathyergus* 3–3.5 mm. Moreover, we have shown in fig. 1, that in fetal stages of *Bathyergus* the eyeballs are still relatively larger, and we cannot see the eyes to be in spatial conflict with the infraorbital muscle.

The assumption that the Bathyergidae are primarily hystricomorphous rodents is further supported by other comparative data (LUCKETT and HARTENBERGER 1985) as well as by the fossil record. Leaving aside the problematical *Tsaganomys* from the Oligocene of Mongolia (MATTHEW and GRANGER 1923), the only fossils which certainly belong to the family Bathyergidae (*Bathyergoides* and *Proheliophobius* from the Miocene of East Africa, LAVOCAT 1973), show a distinct hystricomorphy. The arguments of WOOD (1985) in favour of a convergent development of this character in both *Cryptomys* and the Miocene fossils are not convincing to us. It seems more likely that all of the 'African Hystricognaths' were primarily hystricomorphous. Our results seem to strengthen the view that the Hystricognathi really constitute a monophyletic group of rodents including the problematical Bathyergidae.

Zusammenfassung

Die Hystricomorphie der Bathyergidae, nachgewiesen durch ontogenetische Befunde

Bei je einem jüngeren Foeten von *Bathyergus janetta* und *Georychus capensis* wurde im Canalis infraorbitalis ein Muskelbündel des M. zygomaticomandibularis anterior nachgewiesen. Bei adulten Bathyergidae fehlt ein solcher Muskel mit Ausnahme von *Cryptomys hottentotus*. Die offene Streitfrage, ob die Bathyergidae primär ‚protrogomorph' oder ‚hystricomorph' seien, wird aufgrund der beobachteten embryonalen Relikte im Sinne der letzteren Annahme beantwortet. Nach dieser Auffassung steht einer Zuordnung der Bathyergidae zu den übrigen hystricognathen und hystricomorphen Nagern nichts im Wege.

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Reproductive biology of *Thryonomys swinderianus* (Temminck)

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Abstract

Research done on female cane rats led to the assumption that a vaginal closure membrane does not occur in these animals. These results are in contrast to evidence in the literature. Changes in the vulva as well as a periodical appearance of a vaginal scab could not be brought into connection with the oestrous.

♀♀ with "open vagina" and "secretion" showed no lordose-reaction.

Introduction

We have attempted to show a possible correlation between the visible conditions in the vagina and the related state of oestrous in the cane rat – *Thryonomys swinderianus* –, similar to the changes in the anogenital region during oestrous, which can be observed in a number of myomorph and sciuromorph rodents.

1812 le Gallois (quoted by Weir 1974) first described a vaginal closure membrane in the guinea-pig (Caviidae), a species, which, as *T. swinderianus* also belongs to the suborder Hystricomorpha (Thenius 1980). This membrane has been described by Stockhard and Papanicolaou (1919) as an almost transparent epithelial cellular membrane. They also proposed a direct correlation between the periodical appearance and disappearance of the vaginal closure membrane and the oestrous of the guinea-pig.

Weir (1974) has shown that 29 of 30 observed hystricomorph rodents possessed the vaginal closure membrane and Asibey (1974) confirmed the existence of a vaginal closure membrane in pregnant females of *T. swinderianus*.

Oduor-Okelo and Gombe (1982) have also reported a vaginal closure membrane in the cane rat.